NEW GEOGRAPHICAL AND MORPHOLOGICAL DATA FOR SIDEROXYLON RECLINATUM SUBSPECIES AUSTROFLORIDENSE (SAPOTACEAE), A TAXON ENDEMIC TO SOUTHEASTERN PENINSULAR FLORIDA, U.S.A.

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ABSTRACT

Sideroxylon reclinatum Michx. subspecies austrofloridense (Whetstone) Kartesz & Gandhi is re-diagnosed in light of new morphological data, compared with its presumed closest relatives, and the extent of its distribution is clarified. Sideroxylon reclinatum subsp. austrofloridense is endemic to subtropical rockland habitats of extreme southeastern peninsular Florida, U.S.A. These habitats face threats from exotic species invasions, fire suppression, and sea-level rise due to climate change. Sideroxylon rufohirtum Herring & Judd, sometimes considered a subspecies of S. reclinatum Michx., is here recognized as a separate species.

RESUMEN

Se vuelve a diagnosticar *Sideroxylon reclinatum* Michx. subspecie *austrofloridense* (Whetstone) Kartesz & Gandhi a la luz de nuevos datos morfológicos, comparados con los de sus presuntos parientes más próximos, y se clarifica la extensión de su distribución. *Sideroxylon reclinatum* subsp. *austrofloridense* es endémico de hábitats rocosos subtropicales del extremo sureste peninsular de Florida, U.S.A. Estos hábitats se enfrentan a amenazas de invasiones de especies exóticas, supresión por fuego, y elevación del nivel del mar por cambio climático. *Sideroxylon rufohirtum* Herring & Judd, a veces considerado como subespecie de *S. reclinatum* Michx., se reconoce aquí como una especie diferente.

INTRODUCTION

Sideroxylon L. (Sapotaceae) is a pantropical genus comprising ca. 80 species, occurring most abundantly in tropical America, but also in Macaronesia, Africa, Madagascar, and the Mascarene Islands, with few species in southeast Asia (Govaerts et al. 2001; Smedmark & Anderberg 2007). Prior to Pennington's monographs of the Sapotaceae (1990, 1991), the Neotropical species of Sideroxylon, centered in the Caribbean and Central America and extending into the temperate southeastern U.S., were split among the genera Bumelia Sw., Dipholis A.DC., and Mastichodendron (Engl.) H.J. Lam. The species endemic to the continental U.S. (and extreme northern Mexico) were assigned to Bumelia, along with many tropical taxa (Cronquist 1945, 1946, 1949). They are trees and shrubs of mainly dry habitats, usually armed with thorns, with leaves alternate, often becoming fascicled on short shoots (brachyblasts), inflorescences fasciculate, axillary or in axils of fallen leaves, flowers with a single whorl of quincuncial sepals, corolla lobes with a median segment and two lateral segments, petaloid staminodes alternating with epipetalous stamens, and the seed having its hilum scar in a basal position, with endosperm scanty or lacking (Cronquist 1945). Bumelia was revised by Gray (1886), Small (1900), Clark (1942), and Cronquist (1945, 1949), all of whom differed concerning the number of U.S. species. Pennington (1990) transferred all of Bumelia, Dipholis, and Mastichodendron to a broadly circumscribed Sideroxylon, and for species limits he generally followed Cronquist, recognizing eight U.S. species. More recently, phylogenetic analyses using both morphological and molecular data have shown that Sideroxylon sensu Pennington is monophyletic including Argania from Morocco (Anderberg & Swenson 2003; Swenson & Anderberg 2005; Smedmark et al. 2006), but excluding two taxa from the Arabian peninsula and Socotra (Smedmark & Anderberg 2007; Gautier et al. 2013; Stride et al. in press). Although relationships among the major subclades of *Sideroxylon* are unclear, molecular phylogenies reveal two well-supported Neotropical subclades, one corresponding to *Dipholis/Mastichodendron*, and the other to *Bumelia*, including the species endemic to North America (Smedmark & Anderberg 2007; Stride et al. in press).

Currently eleven species of *Sideroxylon* are recognized in the continental United States (Govaerts et al. 2001; Allison 2006; Wunderlin & Hansen 2008). Of these eleven species, eight are endemic to an area encompassing much of the southeastern U.S. and a bit of extreme northern Mexico, most being concentrated on the coastal plain from Texas through the Carolinas, with Florida as their center of diversity (Govaerts et al. 2001; Allison 2006; Wunderlin & Hansen 2008). These eight are: *Sideroxylon alachuense* L.C. Anderson, *S. lanugino-sum* Michx., *S. lycioides* L., *S. macrocarpum* (Nutt.) J.R. Allison, *S. reclinatum* Michx., *S. rufohirtum* Herring & Judd, *S. tenax* L., and *S. thornei* (Cronquist) T.D. Penn. The above-listed taxa, which likely form a monophyletic group (Smedmark & Anderberg 2007; Corogin and Judd, unpublished DNA sequence data), are distinguished morphologically from their tropical congeners by having a combination of fascicled leaves, conspicuously reticulate tertiary venation, short styles, small fruits, and a bipartite hilum scar (Pennington 1990). Common names include "buckthorn," "bully," and "bumelia."

Sideroxylon reclinatum is a mostly low-growing thorny shrub (occasionally a small tree) of calcareous or sandy, wet to mesic wooded habitats of Florida and the outer coastal plain from southern Georgia to Louisiana. Cronquist (1945) recognized two varieties, *Bumelia reclinata* (Michx.) Vent. var. *reclinata*, and *B. reclinata* var. *rufotomentosa* Cronquist, the latter having been previously recognized as a species (*B. rufotomentosa*) by Small (1900). Whetstone (1985) named a third variety, *B. reclinata* var. *austrofloridensis* Whetstone ("Everglades buckthorn"), based on morphologically distinct collections from subtropical rocklands in the vicinity of Long Pine Key in the Florida Everglades. Varieties *rufotomentosa* and *austrofloridensis* were transferred to *Sideroxylon* by Kartesz and Gandhi (1990), and recognized as *S. reclinatum* subsp. *rufotomentosum* (Small) Kartesz & Gandhi, and *S. reclinatum* subsp. *austrofloridense* (Whetstone) Kartesz & Gandhi, respectively. Based on consistent differences in morphology, habit, and habitat, Herring and Judd (1995) recognized *S. reclinatum* subsp. *rufotomentosum* as a distinct species, *Sideroxylon rufohirtum* Herring & Judd, (see Godfrey 1988), and this designation is here recognized. *S. reclinatum*, *S. rufohirtum*, and a third species, *S. macrocarpum* (Nutt.) J.R. Allison, are here referred to as the *Sideroxylon reclinatum* complex, as they share many similarities in morphology and habit and are traditionally presumed closely related. We discuss how *S. reclinatum* subsp. *austrofloridense* is distinguished from *S. reclinatum* subsp. *reclinatum*, and also from the other two species in the complex.

Our close examination of specimens including more recent collections, along with field observations of both *S. reclinatum* subsp. *reclinatum* and *S. reclinatum* subsp. *austrofloridense*, reveal that the two subspecies are most reliably distinguished by differences in the micromorphology of the abaxial leaf epidermis, and that the extent of distribution of subsp. *austrofloridense*, while limited to extreme southern peninsular Florida, is somewhat larger than was previously supposed.

The focus of this paper is the southern Florida subtropical rockland populations of *Sideroxylon reclinatum* that form subspecies *austrofloridense*. Our aim is to present new morphological and geographical data on these populations, to revise the circumscription and range of the subspecies in light of this new data, to compare the subspecies with its presumed closest relatives, and to discuss its importance and conservation status as part of the endemic flora of southern Florida rockland habitats. A comprehensive taxonomic treatment of *S. reclinatum*, including both subspecies, will be presented in an upcoming revision of the clade of *Sideroxylon* endemic to the continental U.S. and extreme northern Mexico.

MATERIALS AND METHODS

The morphological findings of this study are based on close examination of numerous specimens, both fresh and dried. Dried flowers were rehydrated by boiling in water, and dissected with the aid of a Wild M5A dissecting microscope (Aarau, Switzerland). Dimensions of trichomes were measured with the aid of a Carl Zeiss

Corogin and Judd, Sideroxylon reclinatum ssp. austrofloridense

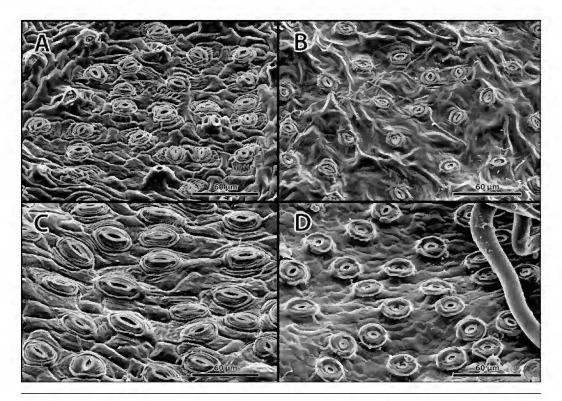
4311036 compound microscope. Scanning electron microscopy (SEM) was employed for examination of leaf surface micromorphology. Leaf material from dried herbarium specimens of taxa being compared was mounted on carbon adhesive tabs on aluminum specimen mounts. Samples were rendered conductive by coating with a gold-palladium alloy in argon vacuum for 90 seconds using a Denton Desk V sputter coater (Denton Vacuum, Moorestown, NJ, USA). Samples were examined with a Hitachi S-4000 field-emission scanning electron microscope (Hitachi High Technologies America, Inc. Schaumburg, IL), and digital micrographs were acquired with PCI Quartz software. SEM work was conducted at the Electron Microscopy Core of the Interdisciplinary Center for Biotechnology Research (ICBR) at the University of Florida. From *Sideroxylon reclinatum* subsp. *austrofloridense*, twelve individuals of each taxon were sampled; from *S. rufohirtum* and *S. macrocarpum*, five individuals of each taxon were sampled. Conclusions regarding the geographical range of *Sideroxylon reclinatum* subsp. *austrofloridense* are based on extensive field observations and data from herbarium specimen labels.

RESULTS AND DISCUSSION

Morphology.—The species of the *Sideroxylon reclinatum* complex share some morphological similarities such as low habit, small leaves with prominent vein reticulum, and abaxial leaf pubescence that is usually sparse, if present, and often deciduous. They are *Sideroxylon reclinatum*, *S. macrocarpum*, and *S. rufohirtum*. *Sideroxylon reclinatum* ranges throughout Florida, southwestern Georgia, and westward along the coastal plain to Louisiana, growing in mesic to wet, sandy to calcareous habitats. This species is not typically highly clonal, is generally low-growing but can reach heights of ca. 3 m as many-trunked shrubs or occasionally small trees, and has small fruits (10 mm diameter or less). It is usually a glabrous plant, any leaf or young stem pubescence quickly deciduous, except for the south Florida subspecies *austrofloridense*, in which pubescence can be persistent. *S. macrocarpum* is a low-growing, highly clonal shrub narrowly endemic to a few counties in southeast Georgia. It is similar in habit and habitat to *S. rufohirtum*, a putative close relative endemic to a few counties in north and west peninsular Florida (Allison 2006). These two species prefer dry sandy habitats, are both highly clonal and low-growing, rarely exceeding 1 m in height, and they have large fruits (> 10 mm diameter), young stems pubescent through the first season, and abaxial leaf pubescence that is sparse and often persistent.

Scanning electron microscope (SEM) images of the abaxial leaf cuticular surfaces of these species (Figs. 1, 2) reveal that the surface features of these taxa are quite distinct from one another. Previous SEM study has shown that taxa of *Sideroxylon* can be distinguished by such characters (Anderson 1996). Stomata in all cases are recessed inside chambers with generally elliptical openings. In both subspecies of *Sideroxylon reclinatum*, each chamber opening is surrounded by a series of irregularly concentric cuticular ridges, often also with ridges radiating out perpendicularly from the opening. The features of *Sideroxylon macrocarpum* and *S. rufohirtum* are rather different from those of *S. reclinatum* (Figs. 1, 2). The stomatal chambers of these species are somewhat larger than those of *S. reclinatum*. In *Sideroxylon macrocarpum*, each elliptic-shaped stomatal chamber of one or more concentric ridges; at least one of these ridges tends to form a striking, neatly defined oval border around the dome. The epidermal surface is strongly patterned, with impressed grooves defining cell outlines. The stomatal structures of *Sideroxylon rufohirtum* are distinctive as well, with stomatal chamber openings centered on conspicuously donut-shaped, broad, flat to slightly cupped, elevated platforms bordered by concentric cuticular ridging, and the cuticular surface between stomata is relatively smooth but with epidermal cell outlines visible and defined by impressed grooves.

At the macromorphological level, the two subspecies of *Sideroxylon reclinatum* are not always easily distinguishable (Table 1). Subspecies *reclinatum* is typically a glabrous plant. Abaxial leaf pubescence, if present at all, tends to be grey to white in color, the trichomes straight or weakly curled, and it is never dense or persistent; trichomes quickly slough off as the leaf matures, persisting only along the abaxial midvein if at all. Sepals and pedicels are glabrous, and the ovary is glabrous or with only a few scattered trichomes at anthesis (Fig. 3). The population of subspecies *austrofloridense* at Long Pine Key in the Everglades is morphologically quite distinct,

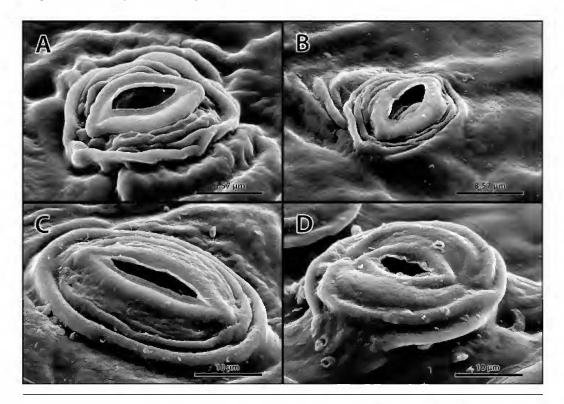


Fi6. 1. SEM images of abaxial epidermal leaf surface of four taxa of *Sideroxylon*, showing differences in stomatal structures and cuticular surfaces. A: S. reclinatum subsp. austrofloridense (*Corogin 1055*, FLAS); B: S. reclinatum subsp. reclinatum (*Corogin 1060*, FLAS); C: S. macrocarpum (Allison 9404, USCH); D: S. rufohirtum (*Corogin 1000*, FLAS). (Magnification 500×).

	subsp. austrofloridense	subsp. reclinatum
Pubescence, abaxial surface of leaf	Sparse to dense, finely wooly, matted, sometimes obscuring leaf surface. Persistent across all of lamina, or quickly deciduous, leaving surface glabrous. Most trichomes strongly curled, ascending, light brown, fading to gray.	Sparse to absent. Quickly deciduous, persistent only along midvein if at all. Trichomes fine, straight to weakly curled, appressed or ascending, light brown to white.
Ovary at anthesis	Sparsely to densely pubescent.	Glabrous or with only a few scattered trichomes.
Sepals at anthesis	Glabrous to densely pubescent.	Glabrous or with only a few scattered trichomes.
Stomatal structures	Cuticular ornamentations around chamber openings are of low to moderate relief.	Cuticular ornamentations around chamber Openings are of moderate to strong relief
Cuticular surface, leaf abaxial (at high magnification)	Epidermal cell outlines always clearly visible and marked by an impressed groove. Surface elaborately ornamented with reticulate pattern in strong relief.	Epidermal cell outlines not always clearly visible, and not marked by an impressed groove. Surface generally smooth and irregularly undulating.

TABLE 1. Comparison of key morphological differences between Sideroxylon reclinatum subsp. austrofloridense and S. reclinatum subsp. reclinatum.

readily distinguishable at a glance from subspecies *reclinatum* by the persistent matted wooly brown pubescence on the abaxial leaf surfaces and often also on the sepals and pedicels, and the ovary is densely to sparsely pubescent at anthesis (Fig. 3). Whetstone (1985) diagnosed subspecies *austrofloridense* based on specimens having these features. But our examination of many south Florida specimens, and recent observations in the field, indicate that plants from locations outside of Long Pine Key (and even a few at Long Pine Key) have a



Fi6. 2. SEM close-up views of stomatal structures of four taxa of *Sideroxylon*. At magnification 3500×; **A:** S. reclinatum subsp. austrofloridense (Corogin 1055, FNPS); **B:** S. reclinatum subsp. reclinatum (Godfrey 81581, FTG). At magnification 3000×; **C:** S. macrocarpum (Allison 9404, USCH); **D:** S. rufohirtum (Ward 1206, FLAS). Note the relative sizes—structures of S. macrocarpum and S. rufohirtum are somewhat larger than those of S. reclinatum subsp. austrofloridense and S. reclinatum subsp. reclinatum.

sparser and less persistent leaf indumentum, appearing nearly glabrous, many of them most closely resembling subspecies *reclinatum*. Whether pubescent or glabrous, however, all of the plants within the range of subspecies *austrofloridense* exhibit characters at the micromorphological level that distinguish them from plants outside this range. It turns out that the two subspecies are most reliably distinguishable by differences in epidermal and cuticular patterns of the abaxial leaf surface (Table 1). These features are visible with good lighting using a high-quality dissecting microscope (such as the Wild M5A) at 1000×, but scanning electron microscopy reveals these features in dramatic clarity. In subspecies *austrofloridense* (Fig. 4), the cuticular features are of moderate to strong relief, and the surface between stomata is elaborately ornamented with a reticulating pattern of grooves and ridges. Epidermal cell outlines are always prominently visible and marked by an impressed groove or by a ridge with a groove within it (See arrows, Fig. 4). In subspecies *reclinatum*, by comparison (Fig. 5), the cuticular ornamentations are of low to moderate relief, and the surface between stomata is relatively smooth and irregularly undulating. Epidermal cell outlines, if visible, are marked by raised ridges that lack an impressed groove along their middle (See arrows, Fig. 5). Thus at the micromorphological level it is easy to distinguish the two subspecies.

KEY TO SPECIES OF THE SIDEROXYLON RECLINATUM COMPLEX

1. Plants highly stoloniferous, often forming clonal patches, aerial shoots rarely more than 1 m tall; fruit 10–14 mm long, plant of dry sandy habitats.

2. Pubescence on young twigs dense, rusty dark red-brown, often persisting well past the first season; abaxial pubescence



Fi6. 3. (A–B): Ovary, A: Sideroxylon reclinatum subsp. reclinatum; B: S. reclinatum subsp. austrofloridense. (C–D): Flowering twig; C: S. reclinatum subsp. reclinatum; D: S. reclinatum subsp. austrofloridense. E–H: S. reclinatum subsp. austrofloridense, Long Pine Key, Everglades National Park, E: Shrub in marl prairie, ca. 1.5 m tall (pine rockland in background); (F) Flowering branch; (G) Fruiting branch; (H) Older branch, ca. 3 cm diameter, with leaves and flowers on brachyblasts.

on young leaves rusty red-brown, sparse to moderately dense, giving surface a distinctly reddish hue; staminodes	
nearly as long as median corolla lobes; ovary densely pubescent; seed variegated; stomatal chamber openings	
located on raised, round, donut- shaped platforms	S. rufohirtum
2. Pubescence on young twigs moderate to dense, blonde to light brown, rarely persisting past the first season; abaxi-	
al pubescence on young leaves blonde to light brown, sparse; staminodes only $\%$ to $\%$ the length of median corolla	
lobes; ovary glabrous or with a few trichomes medially; seed uniformly brown; stomatal chamber openings atop	
raised elliptical domes neatly bordered by one or more concentric ridgesS.n	macrocarpum
Plants not highly stoloniferous, growing as erect shrubs with one to several stems, or occasionally small trees, often	
taller than 1 m; fruit 7–10 mm long, plant of mesic to wet habitats	S. reclinatum

Delimitation of the subspecies of Sideroxylon reclinatum.—It can be seen that Sideroxylon reclinatum subsp. austrofloridense is easily and reliably diagnosable from *S. reclinatum* subsp. reclinatum by a set of distinct character state differences at the micromorphological level. At the macromorphological level, the distinction is less reliable, as glabrescent specimens of subspecies *austrofloridense* can be confused with the typically glabrous subspecies reclinatum. The two taxa are also separated eco-geographically. The more widespread subspecies reclinatum ranges in coastal plain areas from south Georgia west to Louisiana, and throughout Florida as far south as Broward County in the east, and Collier and Monroe Counties in the west, and its habitats feature sandy soils often with limestone near the surface. Subspecies *austrofloridense*, on the other hand, is a narrow endemic, its range restricted to subtropical rockland and marl prairie habitats in a well-defined area of extreme southeast peninsular Florida, and its habitats feature exposed limestone, or limestone thinly overlain with clayey marl soils. All specimens we examined that were collected within the range of subspecies *austrofloridense*, whether glabrous or pubescent, exhibit the unique micromorphological cuticular surface characters described above (Figs. 4, 5). The only place where plants of both micromorphological types occur together is

1.

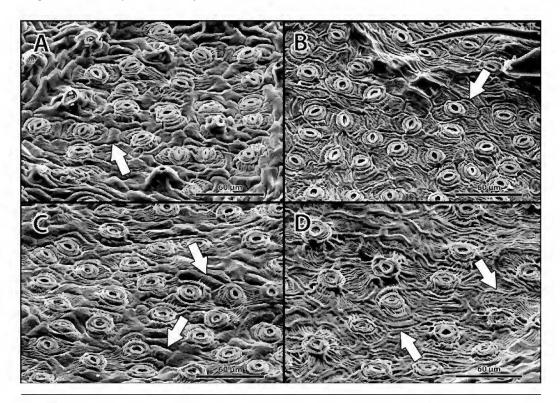


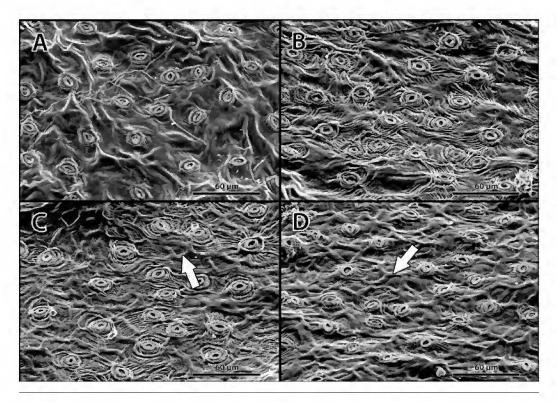
Fig. 4. SEM images of abaxial leaf surface of four different individuals of Sideroxylon reclinatum subsp. austrofloridense. A: Corogin 1055 (FNPS), Long Pine Key, Everglades National Park; B: Possley 67 (FTG), urban Miami-Dade County, FL, Larry & Penny Thompson Park; C: Bradley 1547 (FTG), Collier County, FL, near Monument Lake, Big Cypress National Preserve; D: V.I. Sullivan s.n. (FTG), Long Pine Key, Everglades National Park. Note that epidermal cell outlines are defined in all cases by an impressed groove or a ridge with an impressed groove within it (see arrows). (Magnification 500×).

where the ranges of the two subspecies come into contact, at the western fringes of the range of subspecies austrofloridense, in Big Cypress National Preserve (Fig. 6). The two subspecies are thus clearly defined, and essentially allopatric. Because S. reclinatum subsp. austrofloridense is a narrow endemic restricted to a particular habitat and geographical area, and because it is allopatric with respect to subspecies reclinatum and diagnosable from it, we consider *Sideroxylon*. reclinatum subsp. austrofloridense to be worthy of taxonomic recognition. Since the diagnosing characters are micromorphological and somewhat cryptic, and pubescence characters intergrade, we consider recognition at the subspecific rank to be appropriate. Thus the current classification of these plants is maintained, but the distribution of subspecies austrofloridense is broadened, and it is best diagnosed by the newly discovered micromorphological features.

KEY TO THE SUBSPECIES OF SIDEROXYLON RECLINATUM

1. Young twigs and leaves glabrous or sparsely pubescent with quickly deciduous, fine, blonde to light brown trichomes; mature leaves glabrous or with a few blonde to light brown trichomes persisting along midvein; sepals, pedicels and ovary glabrous or with very few pale trichomes; abaxial leaf epidermal cell outlines obscure, or if visible, defined by raised ridges that lack an impressed groove along their middle._ S. reclinatum subsp. reclinatum 1. Young twigs and leaves densely to sparsely pubescent with brown, finely wooly trichomes; mature leaves glabrous to densely pubescent across abaxial lamina with finely wooly, matted, brown to grey indumentum; sepals, pedicels, and ovary glabrous to densely pubescent with brown trichomes; abaxial epidermal cell outlines always clearly visible, strikingly defined by impressed grooves, or raised ridges with impressed grooves along their middle _ S. reclinatum

subsp. austrofloridense

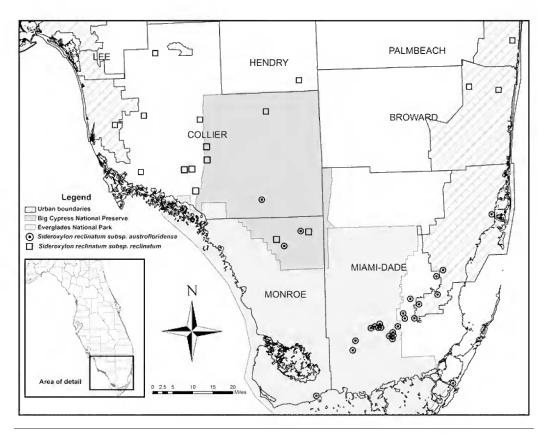


Fi6. 5. SEM images of abaxial leaf surface of four different individuals of *Sideroxylon reclinatum* subsp. *reclinatum*. A: *Corogin 1060* (FLAS), Gilchrist County, FL; B: *Godfrey 81312* (FLAS), Taylor County, FL; C: *Correll 42244* (FTG), Monroe County, FL, at Pine Crest in Big Cypress National Preserve; D: *Godfrey 81581* (FTG), Columbia County, FL. Note that epidermal cell outlines, if visible at all, are defined by raised ridges without the presence of an impressed groove (see arrows). (Magnification 500×).

TAXONOMIC TREATMENT

Sideroxylon reclinatum Michx. subsp. austrofloridense (Whetstone) Kartesz & Gandhi, Phytologia 68:425. 1990. Bumelia reclinata (Michx.) Vent. var. austrofloridensis Whetstone, Ann. Missouri Bot. Gard. 72:545. 1985. Type: U.S.A. Florida. Dade Co.: Everglades National Park, 7 July 1984, R.D. Whetstone 14459 (HOLOTYPE: JSU).

Shrub, single to many-stemmed, occasionally a small tree, ca. 0.5–3.5 m tall, trunk diameter ca. 1–7 cm. Indumentum of unicellular, light brown to grey-white, occasionally red-brown, T-shaped trichomes, symmetric or asymmetric, terete and hollow to flattened in cross-section, having a short stalk and a longer upper portion of varying length, the upper portion curled and ascending. Vegetative buds densely wooly-pubescent with short, curled, ascending, red-brown T-shaped trichomes, the stalk 0.025–0.06 mm, the upper portion 0.2–0.6 mm. Young twigs (long shoots) terete, sparsely lanulose to glabrate, quickly becoming glabrous, smooth, redbrown, prominently dotted with lenticels; thorns often present at nodes, especially on young stems, 3–20 mm long, some becoming short spur shoots or lengthening to become side branches. Mature twigs glabrous, the smooth outer surface becoming longitudinally fissured and fading to very light grey by the second season, becoming rough and gnarled in subsequent seasons, transverse fissures appearing along with deepening longitudinal fissures, giving bark of older stems a somewhat rectangularly-plated reticulate appearance, the leaves clustered on stumpy brachyblasts (short shoots), internode length 7–33 mm. Leaves with petiole 4–5 mm long on young long shoots, 2–4 mm on short shoots, the petioles glabrous or sometimes with a wooly indumentum, light brown and moderately dense to sparse on young petioles, becoming grey-white and sparse on older petioles; blade 29–50 mm long, 16–21 mm wide, rhombic to elliptic to obovate on young long shoots, 8–52 mm



Fi6. 6. Distribution of Sideroxylon reclinatum subsp. austrofloridense (circled dots) and S. reclinatum subsp. reclinatum (squares). The range of S. reclinatum subsp. austrofloridense is centered on the Miami rock ridge, with outliers historically as far south as Key Largo and Flamingo, and more recently as far west and north as Big Cypress National Preserve. Map shows vouchered occurrences only.

long, 5–19 mm wide, narrowly obovate to elliptic (on short shoots), coriaceous, the apex rounded to emarginate, the base cuneate to acute, the margin entire, blades of mature leaves often markedly involute; venation pinnate and conspicuously finely reticulate, brochidodromous, with secondary veins slightly decurrent, branching off midvein in opposite to alternate arrangement, more or less in 6-10 irregularly spaced pairs, with an intersecondary vein occasionally occurring between secondaries, the tertiary and quaternary veins irregular-reticulate, the quinternary veins irregular-reticulate to freely ramifying, areolation moderately developed, the marginal ultimate venation looped; adaxial surface dark green, semi-glossy, sparsely pubescent when young with fine trichomes, becoming glabrous, the veins impressed (fresh leaf) to conspicuously raised (dried leaf), giving the surface a finely textured appearance; abaxial surface glabrous or often sparsely to densely covered with a variably persistent finely wooly indumentum, on young leaves light brown, sparse to moderately dense and matted, often at least partially obscuring the leaf surface, on older leaves fading to grey-white and becoming less dense to glabrate, the trichomes T-shaped, with stalk 0.02-0.08 mm long, upper portion 0.3–1.5 mm long, the upper portions mostly curled and ascending, abaxial epidermal cell boundaries evident under high magnification and marked by impressed grooves, the veins flush to slightly raised (fresh leaf) to raised (dried leaf). Inflorescence a fascicle borne in a leaf axil, these often clustered on short shoots in axils of fallen leaves, each cluster having 3–30 pedicellate flowers, the pedicels 2.5–11.8 mm long, glabrous to densely wooly-strigose at anthesis, often becoming glabrous in fruit. Calyx of 5 (-6) quincuncial, free sepals, the outer two sepals 1.8–2.0 mm long, 1.5–1.7 mm wide, ovate to suborbicular, the apex rounded, the margin entire,

opaque, the inner three sepals 1.8-2.2 mm long, 1.7-2.4 mm wide, orbicular, the apex rounded, the margin entire to erose with broad zone of thin translucent tissue, all sepals glabrous to moderately densely pubescent with light brown to red-brown T-shaped trichomes, the pubescence, if present, wooly on the outer, sericeous on the inner. Corolla white, cyathiform, sympetalous, the tube 1.5-1.8 mm long, enclosed within the calyx, the lobes 5 (-6), exserted and spreading, glabrous, each with a median lobe and two lateral segments, the median lobe 1.5–2.0 mm long, 1.5–2.0 mm wide, orbicular, clawed, cupped around a stamen, the lateral segments 1.8–2.2 mm long (from junction with tube), 1.5–1.8 mm long (from junction with median lobe), 0.7–1.0 mm wide, lanceolate, margins erose, translucent. Stamens 5 (-6), epipetalous, opposite the corolla lobes, exserted; filament 1.4-1.8 mm long, 0.4 mm wide, fixed at top of corolla tube, dilated proximally and narrowing toward anther attachment; anther 1.0-1.1 mm long, sagittate, ventrifixed at the point of the sinus, extrorse, opening by two longitudinal slits. Staminodes petaloid, alternating with stamens, each staminode 2.2 mm long, 1.5 mm wide, deltoid to ovate, margin erose, translucent. Ovary superior, 5-(6-) loculate, locules uniovulate with basal-axile placentation, ovary ca. 1.0-1.3 mm long, 1.0 mm wide, globose to ovoid, tapering abruptly to 1 mmlong style, the ovary at anthesis glabrous to densely pubescent with a sericeous indumentum of straight, appressed, white to slightly tawny T-shaped trichomes, the trichomes longer on distal part of ovary. Fruit a berry, one (rarely 2) - seeded, 6.3–11.0 mm long, 6–10 mm wide, ellipsoid to slightly obovoid to subglobose, black, glossy, glabrous, borne on pedicels 2.5-11.8 mm long. Seeds 4.2-7.0 mm long, 3.6-6.0 mm wide, subglobose to ellipsoid, the testa hard, smooth, glossy, dark to light brown, the color solid to boldly mottled; the hilum scar basal, usually bipartite, the larger part basal, oval to half-moon shaped, 0.8-2.2 mm long, 1.2-2.8 mm wide, with a smaller, laterally elongate part abaxial to the other part, 0.8-2.8 mm long, 0.2-1.2 mm wide, the two parts well-separated by a bridge of testa, the scar being the exposed portion of a hollow cavity under the testa extending a small distance around the basal end of the seed, the cavity filled, especially on the abaxial side, with a yellowish fatty substance.

Distribution and habitat.—Sideroxylon reclinatum subsp. austrofloridense is found only in Miami-Dade, Monroe, and Collier Counties, Florida, where it is restricted to pine rocklands, marl prairies, and edges of tropical rockland hardwood hammocks (Fig. 6). The range of this taxon is centered in Miami-Dade County on the Miami rock ridge, which extends from Long Pine Key in the Everglades northward through urban Miami to the Miami River. It is locally abundant at Long Pine Key, and is found at Pine Island, and around the edges of Royal Palm Hammock and Paradise Key, in Everglades National Park. It has been collected in several extant rockland fragments in the urbanized areas of the Miami rock ridge as far north as the Miami City Cemetery (1944, A. Korsakoff s.n.). Historically, it was collected as far south as Key Largo (1948, C.R. Jackson s.n.) and Flamingo (1924, J.K. Small 11537) in Monroe County. More recently it has been collected farther west and north at locations in Big Cypress National Preserve: Monument Lake in Collier County (2014, Sadle 630; 1998, Bradley 1547), and the Loop Road area (1964, Godfrey 63520) and Lostman's Pines area (2003, Woodmansee 1121) in Monroe County (Hodges & Bradley 2006; Gann et al. 2014). There are unvouchered reports of additional occurrences on the Miami rock ridge and in Big Cypress National Preserve (Gann et al. 2014). All locations where Sideroxylon reclinatum subsp. austrofloridense has been collected have limestone bedrock either exposed at the surface or covered with only a thin layer of marl-based soil. These soils become more sandy toward the northwestern limits of the range, where S. reclinatum subsp. reclinatum is also found.

Phenology.—Flowering April-May, fruit ripening in June-July.

Additional specimens examined: **USA. Florida. Collier Co.**: Big Cypress National Preserve, Monument Lake Campground, 22 Mar 1998, *Bradley 1547* (FTG); Big Cypress National Preserve, Monument Lake Campground, marl prairie E of rd. to campground and N of radio tower service rd., UTM 17N 488611E, 2860886N, 29 May 2014, *Sadle 630* (FNPS). **Miami-Dade Co.**: Everglades National Park, Long Pine Key, 2.5 mi W of campground T5,7S, R37E, SW4 Sec 32, 11 May 1999, *Anderson 18620* (FSU); Everglades National Park, Long Pine Key near Mosier Hammock, 11 May 1999, *Anderson 18621, 18622* (FSU); Everglades National Park, bordering Pine Island Rd., 0.3 mi S of main road, T58S, R37E, SW4 Sec 12, 11 May 1999, *Anderson 18623* (FSU); Frog Pond, just W of C-111 canal, 3.5 miles N of Rt 27, ca. 4 mi W of Florida City, 11 May 1999, *Anderson 18625*, (FSU); Lucille Hammock, 0.9 mi W of 217th Ave., ca. 3 mi W of Florida City, T57S, R38E, SW4 Sec. 29, 11 May 1999, *Anderson 18625* (FSU); Pine Ridge Sanctuary, 21100.SW 300 St., ca. 2 air mi NW of Homestead, 11 May 1999, *Anderson 18631* (FSU); Everglades National Park, Long Pine Key, May 1908, *E.A. Bessey 75* (A); Everglades, Paradise Key, 5 May 1908, *E.A. Bessey 2* (G); Frog Pond, 25°26.837'N, 080°33.757'W, 6 Aug 1997, *Bradley & Woodmansee 422* (FTG); NW of Royal Palm Park, 3 May 1938, *Buswell s.n.* (FTG);

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Everglades National Park, Long Pine Key, N and W of campground, 26 Jul 2011, 25.40341°N, 080.65797°W, Corogin 1045 (FNPS); ibid., 25.40335°N, 080.65838°W, Corogin 1046 (FNPS); ibid., 25.40244°N, 080.66216°W, Corogin 1047 (FNPS); ibid., 25.40138°N, 080.66822°W, Corogin 1048 (FNPS); ibid., 25.40172°N, 080.66997°W, Corogin 1049 (FNPS); ibid., 27 Jul 2011, 25.40463°N, 080.67649°W, Corogin 1050 (FNPS); ibid., 25.40342°N, 080.67348°W, Corogin 1051 (FNPS); ibid., 28 Jul 2011, 25.40359°N, 080.66031°W, Corogin 1052 (FNPS); ibid., 25.40442°N, 080.65965°W, Corogin 1053 (FNPS); ibid., 25.40061°N, 080.66123°W, Corogin 1054 (FNPS); ibid., 25,40061°N, 080.66103°W, Corogin 1055 (FNPS); ibid., 25.40096°N, 080.66393°W, Corogin 1056 (FNPS); ibid., 11 May 2013, 25°24'5.6"N, 080°39'35.9"W, Corogin 1273 (FNPS); ibid., 25°24'6.2"N, 080°39'38"W, Corogin 1274 (FNPS); ibid., 25°24'7.4"N, 080°39'42.9"W, Corogin 1275 (FNPS); ibid., 25°24'6.2"N, 080°40'11.9"W, Corogin 1276 (FNPS); ibid., 26 Jul 2013, 25°24'6.2"N, 080°40'11.9"W, Corogin 1286 (FNPS); Everglades National Park, Long Pine Key, 9 Jul 1961, Craighead s.n. (USF); Everglades National Park, Long Pine Key near Redd Hammock, 22 Dec 1958, Craighead s.n. (FLAS); West Avocado Drive, 15 Feb 1955, F.C.C. 352 (FTG); near Naranja, 21 Jan 1937, Fennell 301 (A); Everglades National Park, Royal Palm Hammock, 6 May 1928, Fisher 54 (US); Everglades National Park, Long Pine Key, 18 Apr 1964, Godfrey 63460 (FSU); Everglades National Park, 3.2 mi N of Rock Reef Pass, 17 Apr 1964, Godfrey 63394 (FSU); Everglades National Park, Long Pine Key, 4 May 1979, Godfrey 77025 (FSU); Everglades, N end Paradise Key, 29 Mar 1909, R.M. Harper 110 (G); Everglades National Park, pinelands auto trail, 1.5 mi W of Long Pine Key rd., 21 Jun 1975, Hill & Harvey 3215 (FTG); Miami City Cemetery, 30 Mar 1944, Korsakoffs.n. (FLAS); Larry & Penny Thompson Park, 25.59887°N, 080.40135°W, 26 May 2004, Possley 67 (FTG); Quail Roost Pineland, 25.57630°N, 080.42754°W, 26 Apr 2011, Possley 109 (FTG); Sunny Palms Pineland, 25.42835°N, 080.52053°W, 26 May 2011, Possley 110 (FTG); Everglades National Park, Paradise Key, 3 May 1920, Rehder 898 (A); Everglades National Park, marl prairie near edge of Royal Palm Road, N of Royal Palm Hammock, UTM 17N 538844E, 2808076N, 28 May 2014, Sadle 627, 628 (FNPS); Everglades National Park, marl prairie adjacent to wet pine rocklands at western edge of Pine Island, just N of Main Park Rd., UTM 17N 541041E, 2808752N, 28 May 2014, Sadle 629 (FNPS); Everglades National Park, Royal Palm Hammock/Paradise Key and vicinity, 21 Sep 1917, Safford & Mosier 22 (US); Everglades, S of Long Key, 18 Jan 1909, J.K. Small & J.J. Carter s.n. (FTG); Hammocks, Homestead to Big Hammock Prairie, 15 Feb 1911, J.K. Small & J.J. Carter s.n. (FTG); Everglades, Camp Jackson to Camp Longview, 21 Feb 1911, J.K. Small & J.J. Carter s.n. (FTG); Everglades National Park, Long Pine Key, 6 May 1904, J.K. Small & P. Wilson s.n. (US); Everglades National Park, Long Pine Key, 5 Apr 1968, Sullivan s.n. (FTG); Everglades National Park, Long Pine Key near picnic ground, 8 Apr 1971, Tomlinson & Avery s.n. (FTG); Everglades National Park, 4.6 mi S of park entrance on main rd. to Flamingo, 23 Apr 1958, Traverse 592 (G); Everglades, Long Pine Key, 5 Jul 1950, Woodbury s.n. (FTG). Monroe Co.: Near Fla. Rt 94, 3.8 mi W of Dade-Monroe County line, 19 Apr 1964, Godfrey 63520 (FSU); Key Largo, 27 Feb 1948, Jackson s.n. (FTG); Hammock back of Flamingo, Cape Sable region, 21 Jul 1924, J.K. Small et al. s.n.(G); Big Cypress National Preserve, Lostmans Pines area, ca. 11.13 km S of Loop Rd. (State Rt 94), 17.9 km W of the Miami-Dade County line, just N of border with Everglades National Park, 25.66063° N, 081.04996° W, 26 Mar 2003, Woodmansee 1121 (FNPS).

Endemism in South Florida rockland habitats.—The southern tip of peninsular Florida, including the Florida Keys, is one of the state's hotspots of rare and endemic plant taxa (Ward 1979; Chaplin et al. 2000). Unusual for the continental United States, the flora of this region is dominated by tropical species of West Indian origin. The uniqueness of Sideroxylon reclinatum subsp. austrofloridense is enhanced by the fact that it is narrowly endemic to the pyrogenic pine rockland habitat of this area. Featuring an overstory of south Florida slash pine (Pinus elliottii Engelm. var. densa Little & Dorman), these rocklands, dotted with small tropical hardwood hammocks and surrounded by marl prairies and marshes, thrive on exposed karstic limestone bedrock only partially covered with the thinnest of soils, at an elevation of only 1-5 m above sea level (Snyder et al. 1990). The understory features a diverse mix of tropical and temperate shrubs, palms, and herbs, with a large number of endemic taxa present in the species-rich herbaceous layer (Loope & Avery 1979; Avery & Loope 1980; Olmsted et al. 1983; Snyder et al. 1990). South Florida pine rocklands share functional, structural, and floristic similarities with tropical rocklands of the Bahamas, Cuba, Hispaniola, and Central America, which are also pyrogenic communities on exposed limestone with a pine overstory, highly diverse understories, and high endemism (Judd 1987; O'Brien et al. 2008; Myers & Rodriguez-Trejo 2009). Although pine rocklands exist in the lower Florida keys, Sideroxylon reclinatum subsp. austrofloridense has never been collected there (Hodges & Bradley 2006). Its known current range is limited to extant rocklands on the mainland, although an early collection from northern Key Largo exists (1948, C.R. Jackson s.n., Fig. 6).

Around thirty plant taxa endemic to south Florida are found in pine rocklands; around a dozen of these are restricted to pine rockland (Avery & Loope 1980; Snyder et al. 1990; Bradley & Gann 1999; FNAI 2010; Gann et al. 2014). Many of these endemics are listed as endangered or threatened at the state or federal level, and several are candidates for listing (Gann et al. 2014). Endemic associates of *Sideroxylon reclinatum* subsp. *austrofloridense* at Long Pine Key include *Chamaesyce deltoidea* (Engelm. ex Chapm.) Small subsp. *pinetorum* (Small) A. Herndon, *C. porteriana* Small, *Euphorbia pinetorum* (Small) G.L. Webster, *Jacquemontia curtisii* Peter ex Small, *Lantana depressa* Small var. *depressa* (Sanders 1987), *Melanthera parvifolia* Small, *Phyllanthus pen-*

taphyllus C. Wright ex Griseb. var. *floridanus G.L.* Webster, *Schizachyrium rhizomatum* (Swallen) Gould, and *Tragia saxicola* Small.

The shrub layer of pine rocklands features more than ninety taxa, mostly of West Indian affinity (Olmsted et al. 1983). Woody associates of *Sideroxylon reclinatum* subsp. *austrofloridense* at Long Pine Key include two species of *Sideroxylon, S. celastrinum* (Kunth) T.D.Penn. and *S. salicifolium* (L.) Lam; both are tropical, ranging from southern Florida into the Caribbean, Mexico, and Central America. *Sideroxylon reclinatum* subsp. *reclinatum* has not been collected in Everglades National Park, but it has been collected in Monroe County at Big Cypress National Preserve (Gann et al. 2014), where the ranges of the two subspecies come into contact.

Other woody understory associates include Ardisia escallonioides Schiede & Deppe ex Schltdl. & Cham., Bourreria cassinifolia (A.Rich.) Griseb., Byrsonima lucida (Mill.) DC., Chiococca alba (L.) A.S. Hitchc., Chrysobalanus icaco L., Chrysophyllum oliviforme L., Coccothrinax argentata (Jacq.) L.H. Bailey, Conocarpus erectus L., Croton linearis Jacq., Dodonaea viscosa Jacq., Forestiera segregata (Jacq.) Krug & Urb., Guapira discolor (Spreng.) Little, Guettarda elliptica Sw., G. scabra (L.) Vent., Ilex cassine L., Metopium toxiferum (L.) Krug & Urb., Morinda royoc L., Mosiera longipes (O. Berg) Small, Myrica cerifera L., Myrsine cubana A. DC., Randia aculeata L., Rhus copallinum L., Tetrazygia bicolor (Mill.) Cogn., and Vachellia farnesiana (L.)Wright & Arn. var. pinetorum (F.J.Herm.) Seigler & Ebinger.

Conservation status.—Sideroxylon reclinatum subsp. austrofloridense is a candidate for federal listing under the Endangered Species Act, under the common name "Everglades Bully" (USFWS 2013a). Although the main population of S. reclinatum subsp. austrofloridense is locally abundant and located on protected land, the U.S. Fish and Wildlife Service considers that a change in listing status is warranted but precluded by higher priorities (USFWS 2013b; Sadle, pers. comm.). The Institute for Regional Conservation in Miami considers Sideroxylon reclinatum subsp. austrofloridense to be imperiled in south Florida (Gann et al. 2002, 2014). The pine rockland plant community is ranked critically imperiled both globally and in Florida by the Florida Natural Areas Inventory (FNAI 2010). The pine rocklands of mainland south Florida once extended from Long Pine Key, the principal upland of Everglades National Park, northeastward along the Miami rock ridge as far as the Miami River, but urban and agricultural development has extirpated the native plant cover from all but Long Pine Key and a handful of small patches on private land or preserved as county parks (Olmsted et al. 1983; Bradley & Martin 2012). The chief immediate threats to Sideroxylon reclinatum subsp. austrofloridense and its habitat are fire suppression and exotic species invasion. Recommended conservation actions currently consist of habitat protection and maintenance by prescribed fire, control of invasive non-native species, efforts to acquire, monitor and protect remaining rockland fragments, and continued monitoring and study to watch for adverse effects that may arise from human activities such as water management policies and the Everglades restoration program (Gann et al. 2002; FNAI 2010; USFWS 2013b).

Long-term sea level rise due to climate change also threatens the rockland flora. Discovery of 8600-yearold submerged remains of pine trees 60 km west of Key West suggests that since the last glacial maximum (ca. 18,000 years before present), south Florida pinelands have been in retreat as rising seas have inundated a once more extensive range; during the past century that retreat has continued measurably in the Florida keys (Ross et al. 1994, 2009). As sea level rises, outright inundation is preceded by saltwater intrusion, which is currently producing changes to the species composition of vulnerable south Florida coastal habitats (Saha et al. 2011). Sea level is predicted to rise 1–2 m by 2100 (URS Corporation et al. 2007; Saha et al. 2011), and elevation at Long Pine Key is 2 m or less. *Sideroxylon reclinatum* subsp. *austrofloridense* and its rare and endemic associates clearly face an uncertain future.

APPENDIX

Additional specimens examined for SEM study, and for the south Florida distribution map (Fig. 6). Additional specimens of these taxa from their entire range were also examined and will be cited in an upcoming taxonomic revision.

Sideroxylon reclinatum Michx subsp. reclinatum.—USA. Florida. Broward Co.: Cypress Creek Hammock near Margate, 28 Apr 1977, Correll 48485 (FTG); Fern Forest Nature Center, Coconut Creek, T59S, R42E, Secs. %, 8 May 2001, Howell 389 (USF). Collier Co.: 2 mi E of Collier-Seminole State Park, by US 41, 1 May 1979, *Godfrey* 77002 (FSU); Cross State Turnpike, Miles City, W of FL 29, 27 May 1966, *Lakela & DeBoer 29857* (USF); Deep Lake, 3 mi N of Jerome, 1 mi E of FL 29, 21 Aug 1965, *Lakela & Laker 29124* (USF); Fakahatchee

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Strand State Preserve, 0.3 mi N of Gate 1, W of James Scenic Drive, 22 May 1999, Pires FS0356 (USF); Fakahatchee, margin of hammock, 6 Mar 1965, Lakela & Long 28181 (USF); off rd. to Bird Sanctuary, Corkscrew, 7 Mar 1965, Lakela & Long 28215 (USF); Kissimmee Billy, N of Alligator Alley, 28 Apr 1976, Correll 47094 (FTG). Flagler Co.: N side of Fla. 305, 5.7 mi E of Volusia Co. line, S32, T13S, R29E, 7 Jul 1965, Ward 4725 (FLAS). Gadsden Co.: Banks of Apalachicola River at Aspalaga, 7 Jul 1955, Godfrey 53598 (G); by County Rd. 269, 0.5 mi from railroad crossing at River Junction, 1 Jul 1991, Godfrey 84198 (TENN); Chattahoochee, bluff along Apalachicola River overlooking Clyde T. Hopkins Municipal Park on River Landing Rd., 8 May 1995, MacDonald 8652 (TENN). Gilchrist Co.: Banks of Suwannee River, near public boat ramp W of Otter Springs, 5 Jun 2012, Corogin 1060 (FLAS); NW of Trenton, ca. 1 mi W of dead-end of County Rd. 344, at Suwannee River, ca. 0.5 mi W of Hart Springs Park, 6 Sep 2003, Judd 8047 (FTG). Hendry Co.: Big Cypress Reservation, 8 May 1959, Sturtevant 146 (US). Lee Co.: Fort Myers, 26 Apr 1934, Buswell s.n. (FTG). Monroe Co.: Big Cypress National Preserve, near Pine Crest, along Loop Rd. 94, 28 Apr 1974, Correll 42244 (FTG). Palm Beach Co.: Yamato Scrub Natural Area, ca. 0.25 mi E of Congress Ave., N of Clint Moore Rd., 26°24.58'N, 80°05.944'W, 12 May 1998, Bradley & Woodmansee 977 (FTG). Taylor Co.: Near Steinhatchee River, by US Rt 98/19, NW of Cross City, 19 May 1984, Godfrey 81312 (FLAS). Sideroxylon macrocarpum (Nutt.) J.R. Allison.—USA. Georgia. Jeff Davis Co: powerline right of way immediately W of Appling Co. line and 0.6 mi from Perry Miller Rd., 31°52.85'N, 82°26.75'W, 26 May 1999, *Nelson 20576* (GA). Laurens Co.: ca. 19.2 air mi SE of Dublin, ca. 9.2 air mi ENE of Cedar Grove, W side of GA Hwy 19, ca. 0.3 road mi S of Buck Creek, 21 Aug 1996, *Allison 9404* (FSU). Pierce Co.: ca. 2 mi NE of Blackshear, N of Shiloh Church, 29 Sep 1999, *Allison 12228* (GA). Tattnall Co.: Gordonia Altamaha State Park, along rd. S of golf course, 32°05'08''N, 082°08'03.8''W, 24 Sep 2012, *Corogin 1179* (FLAS). Wheeler Co.: ca. 11.3 linear mi NNE of Alamo, S side Oconee River, ¼ mi E of GA Hwy 46, 26 Jul 1996, *Allison 9356* (GA).

Sideroxylon rufohirtum Herring & Judd.—USA. Florida. Alachua Co.: Near Kanapaha Prairie southwest of Gainesville, 29.572°N, 082.426°W, 19 Jun 2009, *Corogin1000* (FLAS). Dixie Co.: Lower Suwannee National Wildlife Refuge, Yellow Jacket Loop Rd, 7 May 2004, *Barichivich s.n.* (FLAS). Lake Co.: Roadside on Hwy 19 about 200 yds S of jct with old 441, Tavares, 20 Sep 1971, *Wofford 71-558-A* (TENN). Putnam Co.: 75 yds WNW of intersection of trails #10 and #12, 2000 ft E of Camp Area water tower, Univ. of Florida Conservation Reserve, Welaka, T12S, R26E, 27 Mar 1959, *Ward 1206* (FLAS). Suwannee Co.: T5S, R14E, 519, ca. 5 mi NW of Ichetucknee Springs, ca. 1.5 mi NNE of Beachville, Oct 1981, *Simons s.n.* (FLAS).

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